Wilson Bull., 114(2), 2002, pp. 179–185

NESTING SUCCESS OF THE GREAT CRESTED FLYCATCHER IN NEST BOXES AND IN TREE CAVITIES: ARE NEST BOXES SAFER FROM NEST PREDATION?

KARL E. MILLER[1,2]

ABSTRACT.—Although it is commonly believed that nest boxes yield artificially high estimates of nest success, few investigators have compared nesting success in nest boxes to tree cavities in the same locality during the same time period. I studied nesting success of Great Crested Flycatchers (*Myiarchus crinitus*) breeding in nest boxes and natural sites (i.e., old woodpecker cavities and natural tree hollows) on the same pine plantations in northern Florida. Mayfield estimates of nesting success were nearly identical between nest boxes (0.37 ± 0.05 SE, n = 32 nests) and tree cavities (0.38 ± 0.06 SE, n = 27 nests) during a 2-year period. However, nesting success was greater in nest boxes (0.53 ± 0.06 SE) than in cavities (0.33 ± 0.10 SE) during 1997 and lower in nest boxes (0.26 ± 0.07 SE) than in cavities (0.42 ± 0.09 SE) during 1998. Lower nest success in nest boxes during 1998 was due to increased predation during the incubation period. Nest predation accounted for ≥83% of all nest failures. Documented nest predators included the southern flying squirrel (*Glaucomys volans*) and corn snake (*Elaphe guttata*). Nest boxes and cavity nests did not differ significantly in any habitat variable that would influence nest concealment, nor did these variables differ significantly between years. Evidence suggests that nest predators may learn to exploit nest boxes as a prey resource, either through the development of search images or through long term spatial memory. This study demonstrates that nest boxes are not always safer sites than tree cavities and that static comparisons may give misleading results. *Received 30 July 2001, accepted 25 March 2002.*

Ornithologists have used nest boxes to study avian life histories and population dynamics for more than half a century. However, the use of nest boxes as research tools has been criticized (Møller 1989). Some have argued that nest boxes are safer from predators than natural nest sites and that patterns of reproductive success observed in nest box studies may be an artifact of nesting in boxes (Nilsson 1984, 1986; Møller 1989; Purcell et al. 1997). However, there have been few rigorous field tests of these assumptions. Many studies that purport to show differences between nest boxes and tree cavities have compared separate populations in different locations (e.g., Lundberg and Alatalo 1992, Kuitunen and Aleknonis 1992), while ignoring spatial and temporal differences in habitat quality and predator density. Within a given species, reproductive success can vary considerably over space and time among nest sites (e.g., Nilsson 1975, 1984, 1986; Korpimäki 1984; Alatalo et al. 1988; East and Perrins 1988), prohibiting generalizations about differences between nest boxes and tree cavities.

Few studies have compared the nesting success of birds in nest boxes and tree cavities in the same locality during the same time period, and the results from these have been inconclusive. Although some studies reported higher nesting success in nest boxes (Nilsson 1975, 1986; East and Perrins 1988), others indicated no differences (Robertson and Rendell 1990, Gehlbach 1994) or higher nesting success in cavities (Ritter et al. 1978). Moreover, when differences were found between nest boxes and natural sites, there was no consistent pattern for all cavity-nesting species in a particular study area (Nilsson 1984, Purcell et al. 1997). Furthermore, nest boxes and tree cavities can differ in other respects that often are not measured. Because nesting success of cavity-nesting birds can be correlated with nest height (Nilsson 1984, Li and Martin 1991) and microhabitat structure (Belles-Isles and Picman 1986, Finch 1989), these factors also need to be measured when comparing nest boxes and tree cavities.

My objective in this study was to compare nesting success of Great Crested Flycatchers (*Myiarchus crinitus*) using nest boxes and tree cavities in the same habitats during the same years.

[1] Dept. of Wildlife Ecology and Conservation, Univ. of Florida, Gainesville, FL 32611, USA.

[2] Current address: Bureau of Wildlife Diversity Conservation, Florida Fish and Wildlife Conservation Commission, 4005 South Main St., Gainesville, FL 32601, USA; E-mail: karl.miller@fwc.state.fl.us

METHODS

Study site and study species.—I conducted my study in 35- to 40-year-old slash pine (*Pinus elliottii*) plantations at Camp Blanding Training Site, a Florida Army National Guard facility in northern Florida (30° 00′ N, 82° 00′ W). My field assistants and I monitored nests in tree cavities on twelve 10-ha pine plantation study plots, one 8-ha pine plantation study plot, and one 15-ha pine plantation plot that included patches of turkey oaks (*Quercus laevis*). All study plots were even-aged pine stands lacking a well-developed understory (see Miller 2000 for further description of plant communities). Density of standing dead trees (snags) in these stands ranged from 13–19 per ha. Most snags were <26 cm diameter dbh, decayed rapidly, and persisted for only a few years.

The Great Crested Flycatcher was the most common secondary cavity-nester (i.e., nonexcavator) species on the study area. It is migratory, returning to the study area each year during the last week of March. The Great Crested Flycatcher is single brooded but will renest if its first nesting attempt of the season fails (Lanyon 1997; KEM pers. obs.). Potential nest predators in the study area included the southern flying squirrel (*Glaucomys volans*), cotton mouse (*Peromyscus gossypinus*), corn snake (*Elaphe guttata*), yellow rat snake (*Elaphe obsoleta*), and Blue Jay (*Cyanocitta cristata*).

Nest boxes.—I placed 160 nest boxes on eight of the study plots (20 nest boxes per plot) during late February and early March, 1997. Nest boxes were constructed of rough-cut cedar with an entrance hole (5.1 cm diameter) appropriate for Great Crested Flycatchers. Although the entrance hole allowed occasional use by smaller species, such as the Tufted Titmouse (*Baeolophus bicolor*), Carolina Wren (*Thryothorus ludovicianus*), and Eastern Bluebird (*Sialia sialis*), only the Great Crested Flycatcher commonly used nest boxes. I placed nest boxes on live pine trees at 50-m intervals within each plot, alternating the heights between 1.8 m and 4.8 m above ground. All nest boxes were oriented with the entrance hole facing east by southeast, as an easterly or southeasterly orientation often is preferred by many cavity-nesting bird species (e.g., Conner 1975, McEllin 1979, McFarlane 1992, Rendell and Robertson 1994). I placed each nest box so that the entrance hole was not obscured by vegetation for >1.5 m in all directions.

Nest box monitoring.—I inspected each nest box at least once every 10–14 days during April and May and at least once every 14–20 days during June and early July. As soon as I found nesting activity by Great Crested Flycatchers, I monitored the nest box at 3–4 day intervals. I recorded all other species that occupied nest boxes. Southern flying squirrels were not evicted from nest boxes because they routinely used the same size tree cavities as Great Crested Flycatchers (pers. obs.), and I did not want to bias my comparison of nesting activities in nest boxes versus tree cavities. Because flying squirrels also are potential nest predators, I counted all squirrels observed in each nest box during monitoring visits to assess if flying squirrel densities changed over time. I defined primary roost sites as those nest boxes in which flying squirrels were observed on ≥2 occasions within a season.

Cavity nest monitoring.—I used standard methods (Martin and Geupel 1993) to search for Great Crested Flycatcher nests from mid-April through early July of 1997 and 1998. I also searched a buffer strip approximately 75 m wide around each study plot to ensure that birds breeding on the edges of plantation plots were monitored. I rotated nest search visits among plots and diel periods (early morning, late morning) to maintain comparable search effort among sites. As soon as a cavity nest was located, it was monitored at 3–4 day intervals (Martin and Geupel 1993, Ralph et al. 1993). Nests located <4 m above ground were reached with a stepladder and the contents observed with a light and dental mirror. During 1997, most cavities >4 m high were monitored from the ground through observation of adults carrying nest material or food into the cavity, although I investigated a few cavities in larger, more stable snags with Swedish sectional tree-climbing ladders. During 1998, I monitored all cavities >4 m high with a video probe mounted on a telescoping fiberglass pole (TreeTop II, Sandpiper Technologies, Inc., Manteca, California). I considered nestlings to have fledged if they were alive when checked within 1 day of expected fledging and subsequent checks showed no evidence of predation or disturbance to the nest (Martin et al. 1997). I visited most nest territories 1–2 days after the expected date of fledging to confirm that fledglings were present.

Nest-site characteristics.—I measured structural variables within 0.01-ha circular plots (5 m radius) centered on nests, including percentage of bare ground, percentage of ground covered by grass, percentage of ground covered by shrubs, mean shrub height, mean palmetto (*Serenoa repens*) height, and number of stems 2.5–8.0 cm diameter dbh. Within 0.4-ha circular plots (11.3 m radius), I measured the number of small trees (8–15 cm dbh), total basal area (m^2/ha), canopy height, and midstory height. Methods for collecting habitat data follow Martin et al. (1997).

Statistical analyses.—In analyses of nesting success, I used 14 days and 15 days for the length of the incubation and nestling periods, respectively (Taylor and Kershner 1991; KEM unpubl. data). The day the last egg was laid was considered the first day of incubation. For cavities that were too high to be inspected, I estimated the first day of incubation through observation of parental behavior at the nest (Martin and Geupel 1993). I considered a nest to be successful if it produced ≥1 fledgling. I calculated nesting success rates with the Mayfield method (Mayfield 1961, 1975) as modified by Hensler and Nichols (1981) and Hensler (1985), and tested for differences in nesting success between years and between nest types with one-tailed, standard normal Z tests. I used a Wilcoxon signed rank test (SAS Institute, Inc. 2001) to compare flying squirrel numbers in nest boxes between 1997 and 1998; I

TABLE 1. Mayfield nesting success rates for Great Crested Flycatchers (*Myiarchus crinitus*) using nest boxes, Camp Blanding Training Site, northern Florida.

	Incubation period (14 days)		Nestling period (15 days)		Overall (29 days)	
Year	*n*	Success (SE)	*n*	Success (SE)	*n*	Success (SE)
1997	12	0.917 (0.079)	11	0.578 (0.037)	12	0.531 (0.057)
1998	20[a]	0.446 (0.114)	10	0.582 (0.041)	20	0.260 (0.069)
	$Z = 3.40$, $P < 0.001$		$Z = 0.07$, $P = 0.47$		$Z = 3.03$, $P = 0.001$	

[a] Eight (40%) of these nests were preyed upon within the first 6 days of the incubation period.

tested for changes in (1) the number of nest boxes occupied on each plot, and (2) the maximum number of individuals counted on each plot. I used Kruskal-Wallis tests (MINITAB, Inc. 1996) to compare the heights of successful and unsuccessful nest sites and multivariate analysis-of-variance (MANOVA) tests to compare microhabitat variables around nest sites. Variables recorded as percentages were $(x + 1)^{0.5}$ transformed before analyses.

RESULTS

Nesting success.—During two breeding seasons, I monitored a total of 59 Great Crested Flycatcher nests: 32 in nest boxes and 27 in tree cavities. Most tree nests were in snags in cavities excavated by Red-bellied Woodpeckers (*Melanerpes carolinus*) or Northern Flickers (*Colaptes auratus*), but six (21%) were in natural hollows or crevices in living trees.

Twenty-four of fifty-nine nests (41%) produced ≥1 fledgling. Overall Mayfield nesting success was nearly identical between nest boxes (0.37 ± 0.05 SE) and tree cavity nests (0.38 ± 0.06 SE; $Z = 0.22$, $P = 0.41$). However, annual nesting success was higher in nest boxes (0.53 ± 0.06 SE) than in cavities (0.33 ± 0.10 SE) during 1997 ($Z = 1.77$, $P = 0.039$) and lower in nest boxes (0.26 ± 0.07 SE) than in cavities (0.42 ± 0.09 SE) during 1998 ($Z = 1.42$, $P = 0.078$). Whereas nesting success in tree cavities did not differ significantly between years ($Z = 0.64$, $P = 0.26$), nesting success in nest boxes dropped from 53% during the first year to only 26% during the second year ($P = 0.001$) because of lower nest success during incubation (Table 1). I was unable to continue the experiment for additional years because of extensive tree cutting in several nest box plots during 1999–2000.

Six of the nest boxes used by Great Crested Flycatchers during 1998 had been used previously (five in 1997, one in 1998) either by conspecifics or by Tufted Titmice. Only one of these six nests (17%) was successful, while 5 of the 14 (36%) nests in previously unused nest boxes were successful.

Nest predators.—Nest predation was the most common cause of nest failure, accounting for at least 29 of 35 (83%) nest failures. Three nests failed due to abandonment (two in nest boxes during 1997, one in a snag during 1998). Cause of nest failure was undetermined for three nests in high tree cavities during 1997.

Flying squirrels preyed on three Great Crested Flycatcher nests during the incubation period. In each case, the eggs were broken or missing, the nest was in disarray, and flying squirrels were observed on top of the nest. In addition, many depredated nests in nest boxes were disturbed in a similar fashion during the incubation period but squirrels were not observed subsequently. Corn snakes preyed on two flycatcher nests, one containing five 12-day-old nestlings and the other containing three 13-day-old nestlings; in each case, the snake remained in the nest box for ≥2 days after consuming the nestlings. Although yellow rat snakes were not observed preying on Great Crested Flycatcher nestlings during the study, they did prey on Red-bellied Woodpecker nestlings in the study area (pers. obs.).

Twenty percent of all nest boxes were occupied by flying squirrels as primary roost sites, but I found no evidence that local squirrel populations increased during the study. Maximum number of flying squirrels counted in each plot during the peak Great Crested Flycatcher nesting season (mid-April through May) did not differ significantly between years (Wilcoxon signed rank test, $S = -4.0$, $P = 0.63$). The number of nest boxes occupied by flying squirrels as primary roost sites during spring and summer also did not differ significantly between years (Wilcoxon signed rank test, $S = -6.5$, $P = 0.33$).

Nest-site characteristics.—High and low nest boxes were used by Great Crested Flycatchers in similar proportions during 1997 and 1998 (Fisher's exact test, $P = 1.00$). The ratio of successful to unsuccessful nests did not differ significantly between high and low nest boxes (Fisher's exact test, $P = 1.00$). Height of tree cavity nests did not differ significantly between years (Kruskal-Wallis test, $H = 0.57$, df = 1, $P = 0.45$) or between successful and unsuccessful nests (Kruskal-Wallis test, $H = 0.65$, df = 1, $P = 0.42$). Habitat characteristics around nest sites did not differ significantly between nest boxes and tree cavities (MANOVA, Wilks Lambda = 0.650, $P = 0.35$) or between years (MANOVA, Wilks Lambda = 0.708, $P = 0.43$).

DISCUSSION

This study documented high rates of nest predation in nest boxes. Although nesting success in tree cavities did not differ significantly between years, nesting success in nest boxes was less during the second year because of increased predation during the incubation period (Table 1).

Nest predators.—Direct evidence of nest predation by flying squirrels was found only during the incubation period. Although other researchers have inferred flying squirrel predation on Great Crested Flycatcher nests based on circumstantial evidence collected at 1-week intervals (Taylor and Kershner 1991, White and Seginak 2000), this study confirmed flying squirrel predation on eggs at three nest boxes. Flying squirrels have been reported preying on eggs of other cavity-nesting birds, including Black-capped Chickadees (*Poecile atricapillus*; Stabb et al. 1989) and Red-cockaded Woodpeckers (*Picoides borealis*; R. N. Connor pers. comm., J. J. Kappes pers. comm.). Direct evidence of nest predation by snakes was found only during the nestling period. Snakes generally prey on cavity nests during the nestling period and not during incubation (Laskey 1946; Jackson 1970, 1977; Hensley and Smith 1986; Eichholz and Koenig 1992). Together, these data suggest that snakes were not primarily responsible for the high level of egg predation in nest boxes during the second year of the study.

Nest predator densities.—I assessed whether the availability of nest boxes could have increased local densities of flying squirrels, thereby increasing the odds of a squirrel opportunistically encountering and raiding a flycatcher nest. Both the total number of flying squirrels using nest boxes and the number of nest boxes occupied by one or more squirrels did not change between years, indicating no increase in the movement of squirrels among nest boxes during 1998.

Potential for learning by nest predators.—Several researchers have demonstrated a positive correlation between the risk of nest predation and the age of a nest site, both within (Nilsson et al. 1991) and across (Martin and Li 1992, Martin 1993) cavity-nesting bird species; species and individuals that excavate new nest cavities have lower rates of nest predation than do nonexcavators that rely on old cavities for nest sites. One explanation for this pattern is that nest predators may be more cognizant of locations of older nest sites. Robertson and Rendell (1990) found that nesting success of Tree Swallows (*Tachycineta bicolor*) in nest boxes decreased over time because of increasing predation by raccoons (*Procyon lotor*) and rat snakes. Sonerud (1985a, 1985b, 1989) demonstrated experimentally that pine martens (*Martes foina*) developed long term spatial memory of the locations of nest boxes used by Boreal Owls (*Aegolius funereus*). In Sweden, nest boxes for Common Goldeneyes (*Bucephala clangula*) that were preyed upon in a given year also tended to be preyed upon in successive years (Dow and Fredga 1983).

In this study, predation on eggs in nest boxes increased markedly during the second year of the study. Nest success was highest in new nest boxes (i.e., 1–2 months after installation in 1997) than in older nest boxes or in cavities. Nests in boxes that were reused for a second time were more likely to fail than nests in boxes being used for the first time. Moreover, predation rates on artificial nests placed in nest boxes (after the conclusion of this study) were higher in nest boxes that had been used previously by Great Crested Flycatchers than in nest boxes that had no previous nesting attempts (unpubl. data). These results suggest that nest predators in this study learned to exploit nest boxes as a prey resource, either through the development of long term spatial memory or search images.

Using cameras, Farnsworth and Simons (2000) documented flying squirrels and snakes returning to depredated Wood Thrush (*Hylocichla mustelina*) nests several days after the original predation event. Such observations suggest that a variety of nest predators are capable of learning the locations of profitable prey sites and returning periodically to them. Although flying squirrels probably were responsible for most predation on eggs during 1998, snakes also may have played a role. Taylor and Kershner (1991) observed a small (56-cm) rat snake taking a Great Crested Flycatcher nestling from a nest box 2 days after another nestling had disappeared from the same nest box; they speculated that the snake made return visits because of its relatively small size.

Nest-site characteristics.—Nest boxes and tree cavity nests did not differ significantly in any habitat variable that would influence nest concealment, nor did these variables differ significantly between years. This is perhaps not surprising, given the even-aged, relatively homogeneous structure of the pine plantations. Heights of successful and unsuccessful nests did not differ significantly for nest boxes and cavity nests in either year. Thus, lower nest success in nest boxes cannot be attributed to a difference in the accessibility of these sites to predators, either between nest sites or between years. It is unknown whether nest boxes were more conspicuous than tree cavities because they were mounted externally on the tree trunk, whereas cavities are contained within the tree bole.

Physical dimensions of the nest cavity also did not appear to be responsible for predation differences. Most tree cavities used by Great Crested Flycatchers were old Red-bellied Woodpecker cavities, whose openings range from 5.0–5.7 cm in diameter (Jackson 1976, Shackelford et al. 2000, unpubl. data). Entrances at nest boxes (5.1 cm diameter) were no larger or more accessible than tree cavity nests. Obviously, temporal differences in nest predation in nest boxes were not influenced by cavity entrance size because all nest boxes had the same size entrance hole.

Ectoparasite loads, although not measured, could not have accounted for lower nest success in nest boxes during the second year, because (1) nest boxes were thoroughly cleaned of nesting debris during the intervening winter, and (2) the majority of nest failure occurred because of predation on eggs.

Conclusions.—This study demonstrates that nest boxes are not always safer sites than tree cavities. My results also underscore the importance of looking at temporal dynamics of nest predation, as static comparisons of nest success between natural sites and nest boxes may give incomplete or misleading results. If years were pooled in this study, then one would have concluded that Great Crested Flycatchers had nearly identical nesting success in nest boxes and tree cavities. Many researchers do not report annual differences in nest success and/or nest predation in nest boxes (e.g., Korpimäki 1984, Nilsson 1984, Kuitunen and Aleknonis 1992, Purcell et al. 1997). Other researchers present evidence that nest predation increases over time in nest boxes without discussing the ecological significance of this pattern (e.g., Bellrose et al. 1964, Dugger et al. 1999). When researchers undertake comparisons of breeding ecology in nest boxes and tree cavities, it is important that they report annual changes in these parameters.

Theoretical and empirical evidence indicates that nest predation may increase with the age of a nest box. The predictable, permanent locations of nest boxes may make them more vulnerable than tree cavities to nest predators over the long term (Sonerud 1985a, 1985b, 1989, 1993). Further research is needed to identify the factors—including type of predators (mammal, snake, bird), availability of alternative prey in the study area, persistence times of natural nest cavities in the study area—that determine how predators respond to nest boxes. For example, predation by martens on Boreal Owl nests appears to be influenced by the abundance of alternative prey; in a study area with low rates of nest predation (5%) and abundant microtine rodents, Korpimäki (1987) found little relationship between nest box age and predation rates by martens. I predict that, within a given area, nest predation rates will tend to be higher in nest boxes than in tree cavities if cavities in that area are relatively short-lived (i.e., they do not persist as long as the nest boxes) and nest predators in that area are sufficiently reliant on bird eggs and nestlings in their seasonal diet.

Tree cavities can vary considerably across a species' range or within a study area with respect to height, age, volume, structural integrity, accessibility to predators, and in the densities at which they occur. Nest boxes are useful tools that allow manipulation of many of these factors in controlled experiments, thus facilitating the study of particular mechanisms or ecological relationships that otherwise would be difficult or nearly impossible to study (Koenig et al. 1992). Further use of nest boxes in carefully designed experiments is warranted.

ACKNOWLEDGMENTS

Funding was provided by the Florida Fish and Wildlife Conservation Commission, the North American Bluebird Society, and a Student Research Grant from Sandpiper Technologies, Inc. P. Hall and P. Catlett of the Florida Army National Guard provided logistic support on site. C. McRae, M. Lindberg, L. Hayes, and S. Jones of the Univ. of Florida provided administrative support. E. Tillman and M. Moulton helped assemble nest boxes, and G. Jones, M. Williams, and A. van Doorn assisted with locating and monitoring nests. I thank D. Levey, S. Moegenburg, M. Moulton, K. Sieving, and G. Williams for discussion and reviews of early drafts. The manuscript was improved by the comments of J. Dunning, and W. Taylor. This paper is Journal Series Number R-08289 of the Florida Agricultural Experiment Station, Gainesville.

LITERATURE CITED

ALATALO, R. V., A. CARLSON, AND A. LUNDBERG. 1988. Nest cavity size and clutch size of Pied Flycatchers *Ficedula hypoleuca* breeding in natural cavities. Ornis Scand. 19:317–319.

BELLES-ISLES, J. C. AND J. PICMAN. 1986. Nesting losses and nest site preferences in House Wrens. Condor 88:483–486.

BELLROSE, F. C., K. L. JOHNSON, AND T. U. MEYERS. 1964. Relative value of natural cavities and nesting houses for Wood Ducks. J. Wildl. Manage. 28: 661–676.

CONNER, R. N. 1975. Orientation of entrances to woodpecker nest cavities. Auk 92:371–374.

DOW, H. AND S. FREDGA. 1983. Breeding and natal dispersal of the Goldeneye, *Bucephala clangula*. J. Anim. Ecol. 52:681–695.

DUGGER, K. M., B. D. DUGGER, AND L. H. FREDRICKSON. 1999. Annual survival rates of female Hooded Mergansers and Wood Ducks in southeastern Missouri. Wilson Bull. 111:1–6.

EAST, M. L. AND C. M. PERRINS. 1988. The effect of nestboxes on breeding populations of birds in broadleaved temperate woodlands. Ibis 130:393–401.

EICHHOLZ, M. W. AND W. D. KOENIG. 1992. Gopher snake attraction to birds' nests. Southwest. Nat. 37:293–298.

FARNSWORTH, G. L. AND T. R. SIMONS. 2000. Observations of Wood Thrush nest predators in a large contiguous forest. Wilson Bull. 112:82–87.

FINCH, D. M. 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in House Wrens. Condor 91:848–859.

GEHLBACH, F. R. 1994. Nest-box versus natural-cavity nests of the Eastern Screech-Owl: an exploratory study. J. Raptor Res. 28:154–157.

HENSLER, G. L. 1985. Estimation and comparison of functions of daily nest survival probabilities using the Mayfield method. Pp. 289–301 *in* Statistics in ornithology (B. J. T. Morgan and P. M. North, Eds.). Springer-Verlag, New York.

HENSLER, G. L. AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators, and simulation results. Wilson Bull. 93:42–53.

HENSLEY, R. C. AND K. G. SMITH. 1986. Eastern Bluebird responses to nocturnal black rat snake nest predation. Wilson Bull. 98:602–603.

JACKSON, J. A. 1970. Predation of a black rat snake on Yellow-Shafted Flicker nestlings. Wilson Bull. 82: 329–330.

JACKSON, J. A. 1976. How to determine the status of a woodpecker nest. Living Bird 15:205–219.

JACKSON, J. A. 1977. Notes on the behavior of the grey rat snake (*Elaphe obsoleta spiloides*). J. Miss. Acad. Sci. 22:94–96.

KOENIG, W. D., P. A. GOWATY, AND J. L. DICKINSON. 1992. Boxes, barns, and bridges: confounding factors or exceptional opportunities in ecological studies? Oikos 63:305–308.

KORPIMÄKI, E. 1984. Clutch size and breeding success of Tengmalm's Owl *Aegolius funereus* in natural cavities and nest-boxes. Ornis Fenn. 61:80–83.

KORPIMÄKI, E. 1987. Selection for nest-hole shift and tactics of breeding dispersal in Tengmalm's Owl *Aegolius funereus*. J. Anim. Ecol. 56:185–196.

KUITUNEN, M. AND A. ALEKNONIS. 1992. Nest predation and breeding success in Common Treecreepers nesting in boxes and natural cavities. Ornis Fenn. 69:7–12.

LANYON, W. E. 1997. Great Crested Flycatcher (*Myiarchus crinitus*). No. 300 *in* The birds of North America (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, Pennsylvania, and the American Ornithologists' Union, Washington, D.C.

LASKEY, A. R. 1946. Snake depredations at bird nests. Wilson Bull. 58:217–218.

LI, P. AND T. E. MARTIN. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

LUNDBERG, A. AND R. V. ALATALO. 1992. The Pied

Flycatcher. T & A D Poyser, London, United Kingdom.

MARTIN, T. E. 1993. Evolutionary determinants of clutch size in cavity-nesting birds: nest predation or limited breeding opportunities? Am. Nat. 142: 937–946.

MARTIN, T. E. AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. J. Field Ornithol. 64:507–519.

MARTIN, T. E. AND P. LI. 1992. Life history traits of open- vs. cavity-nesting birds. Ecology 73:579–592.

MARTIN, T. E., C. R. PAINE, C. J. CONWAY, W. M. HOCHACHKA, P. ALLEN, AND W. JENKINS. 1997. BBIRD field protocol. Montana Coop. Wildlife Research Unit, Univ. of Montana, Missoula.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.

MAYFIELD, H. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

MCELLIN, S. M. 1979. Nest sites and population demographies of White-breasted and Pygmy nuthatches. Condor 81:348–352.

MCFARLANE, R. W. 1992. A stillness in the pines: the ecology of the Red-cockaded Woodpecker. Norton, New York.

MILLER, K. E. 2000. Nest-site limitation, nest-site selection, and nest predation in a cavity-nesting bird community. Ph.D. diss., Univ. of Florida, Gainesville.

MINITAB, INC. 1996. MINITAB reference manual, rel. 11 for Windows. Pennsylvania State Univ., State College.

MØLLER, A. P. 1989. Parasites, predators and nest boxes: facts and artifacts in nest box studies of birds? Oikos 56:421–423.

NILSSON, S. G. 1975. Clutch size and breeding success of birds in nest boxes and natural cavities. Var Fagelvarld 34:207–211.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand. 15: 165–175.

NILSSON, S. G. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. Auk 103: 432–435.

NILSSON, S. G., K. JOHNSSON, AND M. TJERNBERG. 1991. Is avoidance by Black Woodpeckers of old nest holes due to predators? Anim. Behav. 41: 439–441.

PURCELL, K. L., J. VERNER, AND L. W. ORING. 1997. A comparison of the breeding ecology of birds nesting in boxes and tree cavities. Auk 114:646–656.

RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. Pacific Southwest Research Station, USDA Forest Service, Albany, California.

RENDELL, W. B. AND R. J. ROBERTSON. 1994. Cavity-entrance orientation and nest-site use by secondary hole-nesting birds. J. Field Ornithol. 65:27–35.

RITTER, F., M. HEIDRICH, AND W. ZEINERT. 1978. Statistische daten zur brutbiologie Thhringer Rauhfusskäuze (*Aegolius funereus* (L.)). Ornithol. Mitt. 24:37–45.

ROBERTSON, R. J. AND W. B. RENDELL. 1990. A comparison of the breeding ecology of a secondary cavity nesting bird, the Tree Swallow (*Tachycineta bicolor*), in nest boxes and natural cavities. Can. J. Zool. 68:1046–1052.

SAS INSTITUTE, INC. 2001. SAS for personal computers, ver. 8.2. SAS Institute, Inc., Cary, North Carolina.

SHACKELFORD, C. E., R. E. BROWN, AND R. N. CONNER. 2000. Red-bellied Woodpecker (*Melanerpes carolinus*). No. 500 *in* The birds of North America (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.

SONERUD, G. A. 1985a. Risk of nest predation in three species of hole nesting owls: influence on choice of nesting habitat and incubation behaviour. Ornis Scand. 16:261–269.

SONERUD, G. A. 1985b. Nest hole shift in Tengmalm's Owl, *Aegolius funereus*, as defence against nest predation involving long-term memory in the predator. J. Anim. Ecol. 54:179–192.

SONERUD, G. A. 1989. Reduced predation by pine martens on nests of Tengmalm's Owl in relocated boxes. Anim. Behav. 37:332–343.

SONERUD, G. A. 1993. Reduced predation by nest-box relocation: differential effect on Tengmalm's Owl nests and artificial nests. Ornis Scand. 24:249–253.

STABB, M. A., M. E. GARTSHORE, AND P. L. AIRD. 1989. Interactions of southern flying squirrels, *Glaucomys volans*, and cavity-nesting birds. Can. Field-Nat. 103:401–403.

TAYLOR, W. K. AND M. A. KERSHNER. 1991. Breeding biology of the Great Crested Flycatcher in central Florida. J. Field Ornithol. 62:28–39.

WHITE, D. H. AND J. T. SEGINAK. 2000. Nest box use and productivity of Great Crested Flycatchers in prescribed-burned longleaf pine forests. J. Field Ornithol. 71:147–152.